African Invertebrates Vol. 44 (1) Pages 185–197 Pietermaritzburg August, 2003

Hitherto undescribed interommatidial exocrine glands in Chilopoda

by

C. H. G. Müller[1], **J. Rosenberg**[2] and **V. B. Meyer-Rochow**[3]

([1]University of Rostock, Institute for Biodiversical Research, General & Special Zoology, Universitaetsplatz 2, D-18051 Rostock, Germany, carsten.mueller@biologie.unirostock. de; [2]Ruhr-University Bochum, Faculty of Biology, Chair of Animal Physiology, PO Box 10 21 48, D-44780 Bochum, Germany, sommerhaus-rosenberg@t-online.de; [3]International University Bremen (IUB), Faculty of Engineering and Science (Biology), Campus Ring 1, D-28759 Bremen, Germany, and Department of Biology, University of Oulu, SF-90014 Oulu, Finnland, b.meyer-rochow@iu-bremen.de *or* vmr@cc.oulu.fi)

ABSTRACT

Pore openings in different arrangements were observed between the ommatidia of the compound eyes of *Scutigera coleoptrata* (Scutigeromorpha) and *Lithobius forficatus* (Lithobiomorpha). Similar pores were not detectable between the ommatidia of either Scolopendromorpha or Craterostigmophora. Fine structural investigations revealed that the pores belong to epidermal exocrine glands. In order to highlight their specific location between the ommatidia, we suggest naming them 'interommatidial exocrine glands'. Their function remains unclear. Possibly these glands produce anti-fungal or anti-bacterial substances which cover the corneae of the facetted eyes and thus preserve their clarity. Alternatively, secretions of the glands could prevent attachment of ectoparasites on the ommatidial cornea. We also discuss the significance of the 'interommatidial exocrine glands' in the light of the current debate on chilopod phylogeny.

INTRODUCTION

The cuticle of all centipedes is traversed by numerous pores that arise from exocrine glands in the epidermis. Until now these glands have received little scientific attention. However some older histological studies of epidermal glands in different regions of the body involved Chilopoda (Grenacher 1880; Brade-Birks & Brade-Birks 1920; Fuhrmann 1922; Koch 1927; Fahlander 1938; Blower 1951 1952), and more recently additional information on their fine structural organisation has been forthcoming. The large ventral or sternal glands of Geophilomorpha (Turcato & Minelli 1990; Hopkin & Anger 1992) and the large telopodal glands of Lithobiomorpha (Keil 1975) are developed in distinct areas where the glands open in clusters of pore openings. Smaller epidermal glands in *Lithobius forficatus* Linnaeus, 1758 are associated with the organ of Tömösvary (Tichy 1973), with sensilla trichoidea, or with the telopodal glands (Keil 1975). Alternatively, they are situated on the coxae of the last four trunk segments (Rosenberg 1994). Exocrine glands are also part of the coxal organs in Chilopoda (Rosenberg 1985; Rosenberg & Greven 1996). In *Scutigera coleoptrata* Linnaeus, 1758 the complex maxillary organ gland is composed of numerous exocrine glands (Hilken *et al*. 2003).

While studying the fine structure of the facetted eye of *S. coleoptrata*, we observed some pore openings between the hexagonal ommatidia. Fine structural investigations revealed that each pore represents the distal part of a single epidermal exocrine gland which has not been described before. Similar epidermal glands in *L. forficatus*, situated between ommatidia of the lateral ocelli were, however, described as integument glands ('Integumentdrüsen') by Grenacher (1880) more than a century ago. Since we now know that the pores represent openings of glands, it is suggested that all of them be named 'interommatidial exocrine glands' to mark their specific arrangement between the ommatidia of the chilopod eye.

One intention of this study was to describe the cellular structure of this new epidermal gland type in *S. coleoptrata*. We also reviewed the observations of Grenacher (1880) on

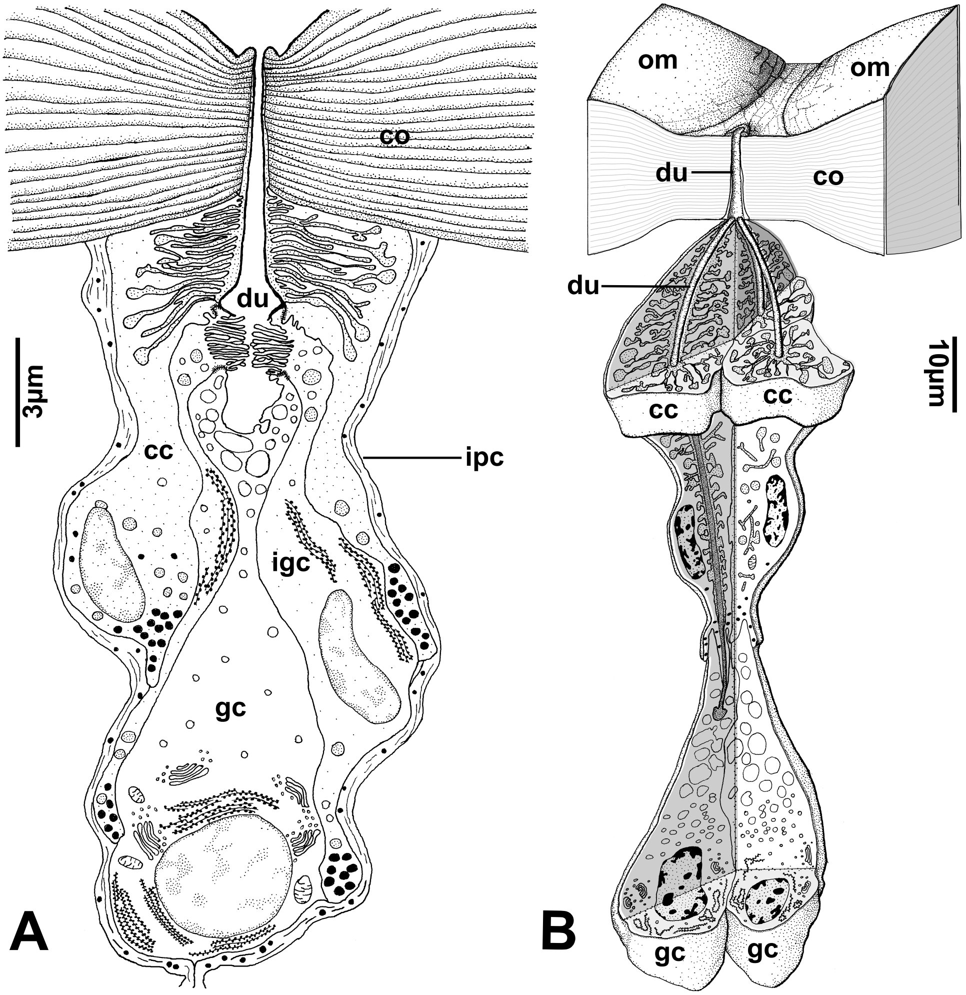


Fig. 1. Semi-schematic reconstruction of two different types of scutigeromorph and lithobiomorph interommatidial exocrine gland. **A.** A longitudinal section through one interommatidial exocrine gland present within the compound eye of *Scutigera coleoptrata*. **B.** The probably more advanced lithobiomorph type, where up to three glandular modules are fused to one single interommatidial exocrine gland (*Lithobius forficatus*, cut-away view). *cc* = canal cell, *co* = cornea, *du* = cuticular gland ductule, *gc* = secretory gland cell, *igc* = intermediary gland cell, *ipc* = interommatidial pigment cell (covering cell), *om* = ommatidium.

L. forficatus and investigated whether similar pore openings of epidermal glands are established between the ommatidia of the so-called lateral ocelli as, for instance in the Scolopendromorpha (Scolopendridae and Cryptopidae) and Craterostigmomorpha.

Besides providing a detailed morphological description, a further aim of this study was to speculate on the significance of the interommatidial exocrine glands in the light of the recently reviewed phylogenetic discussion on whether to follow the ‘Anamorpha concept’ of Attems (1926), the ‘Pleurostigmophora hypothesis’ (e.g. Dohle 1985 1998; Borucki 1996), or the ‘Heteroterga hypothesis’ (Ax 1999). All three of these hypotheses try to explain the relationships within the Chilopoda.

MATERIAL AND METHODS

Scutigera coleoptrata (Scutigeromorpha) and *Scolopendra cingulata* Latreille, 1829 (Scolopendromorpha) were collected from the islands of Šipan (Croatia) and Ibiza (Spain), and *Lithobius forficatus* (Lithobiomorpha) and *Cryptops hortensis* Leach, 1814 (Scolopendromorpha) from a compost heap near Cologne (Germany).

Individuals whose eyes were used in this study were decapitated under dark conditions. The severed head was then split in half along the sagittal plane in buffer solution. For TEM (transmission electron microscopy) investigations the bisected heads were fixed in a cold solution of prefixative modified after Karnovsky (1965) and including 2 % glutaraldehyde, 2 % paraformaldehyde, 1.52 % NaOH and 1.2g d-glucose dissolved in a 2.25 % natriumhydrogenphosphate-buffer (pH 7.4). Prefixation was followed by two hours of fixation in 1 % OsO4 at room temperature by using the same buffer. After dehydration in a graded series of ethanol the head pieces were embedded in epoxide resin (Araldit, FLUKA®). Ultrathin sections were stained with uranyl acetate and lead citrate for five minutes and examined under a ZEISS EM 902A electron microscope.

For SEM (scanning electron microscopy) observations prefixed head pieces (see above) were critical point dried, sputtered with gold and observed at a voltage of 15 kV under a ZEISS DSM 960A electron microscope. SEM investigations on *Australobius scabrior* Chamberlin, 1920 (Lithobiomorpha) and the Tasmanian *Craterostigmus tasmanius* Pockock, 1902 (Craterostigmomorpha) were done by Gregory Edgecombe (Australian Museum, Sydney).

RESULTS

Scanning Electron Microscopy (SEM)

In *S. coleoptrata* pore openings (0.5–0.6 µm) surrounded by a cuticular bulge are arranged between the hexagonal facetted ommatidia (Fig. 2A). The pores are strictly limited to the triangular interstitium which are always formed by a group of three ommatidia (Fig. 2B). An ommatidium in the midst of the eye has an average of two pores, but this number may vary locally. In the lateral regions (dorsal and ventral part of the eye) more pores are observable than in the frontal, caudal or apical eye region. A regular arrangement pattern is not apparent.

In *L. forficatus* and *A. scabrior* similar pore openings are present between the ommatidia of the lateral ocelli (Fig. 2C). With respect to *L. forficatus*, they are, however, considerably wider in diameter (1.0–1.2 µm). Additionally, they are developed in smaller numbers and a cuticular bulge around the pore is not observable. Referring to a total number of 25 single

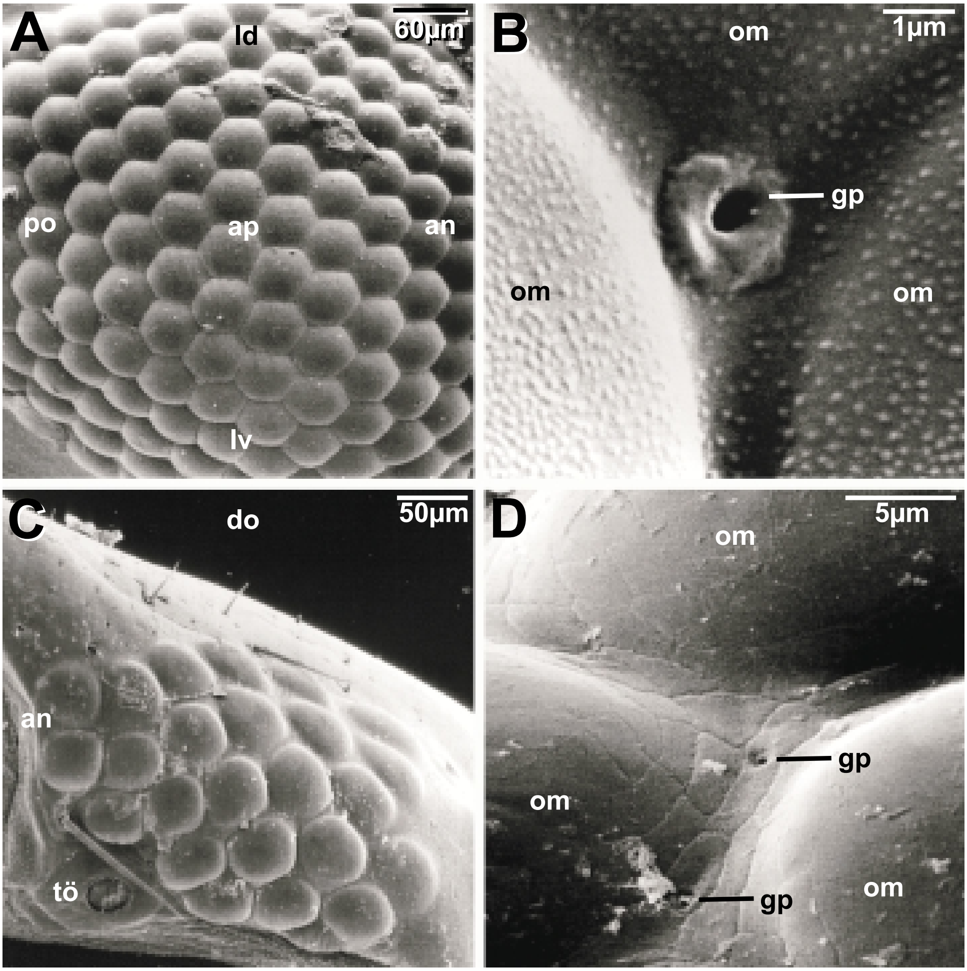


Fig. 2. Scanning electron micrographs (SEM) showing the outer morphology of the compound eyes of *Scutigera coleoptrata* and *Lithobius forficatus*. **A.** Lateral view of right compound eye of *S. coleoptrata*, reproducing fairly dense hexagonal packing of the facets (chosen counting regions marked). **B.** Dorsal view of one triangular interommatidial space, housing one gland pore opening (*S. coleoptrata*). **C.** Lateral view of the left eye of *L. forficatus* representing a lateral field of 25 condensed, sometimes hexagonally arranged, ommatidia. **D.** Antero-lateral view of two interommatidial gland pore openings on the corneal surface of the left eye of *L. forficatus*. *an* = anterior eye region, *ap* = apical eye region, *do* = dorsal, *gp* = interommatidial gland pore, *ld* = latero-dorsal eye region, *lv* = latero-ventral eye region, *om* = ommatidium, *po* = posterior eye region, *tö* = Tömösváry Organ.

ocelli, between four and six pores were observed on each eye (Fig. 2D), but with an average of one pore per ocellus, they are strictly limited to the central region.

Such pore openings are not visible between the four ocelli of *S. cingulata*, nor among the more numerous lenses of *C. hortensis*. The eyes of *C. tasmanius* are represented by only one single pair of ocelli and therefore do not provide sufficient interocellar spaces.

Transmission Electron Microscopy (TEM)

S. coleoptrata **(Scutigeromorpha)**

The pore openings belong to small epidermal exocrine glands. These so-called 'interommatidial exocrine glands' extend from the level of the corneal surface down to the nuclear region of the primary pigment cells. In *S. coleoptrata* each gland is composed of three different cell types: a single secretory gland cell, an intermediary ('accessory') cell and a distal canal cell. Both intermediary and canal cells surround the distal and median parts of the secretory cell in an onion-like manner (see Figs 1A, 3A).

Secretory gland cell

The secretory gland cell is drop-shaped. Its widened basal region houses the nucleus. Abundant cisternae of rough ER with parallel membrane orientation, numerous mitochondria, dictyosomes and large numbers of small electron-lucent and osmiophilic secretory granules are situated around the nucleus (Fig. 3B). Free ribosomes are also observable. The cytoplasm of its distal part is dominated by small and often fused electron-lucent secretory granules (Fig. 3A). The distal part of the cell invaginates into a pear-shaped extracellular cavity. The contents of the secretory granules are discharged into this cavity. *Zonulae adhaerentes* provide a stable link to the adjacent intermediary cell (Fig. 3C).

Intermediary ('accessory') cell

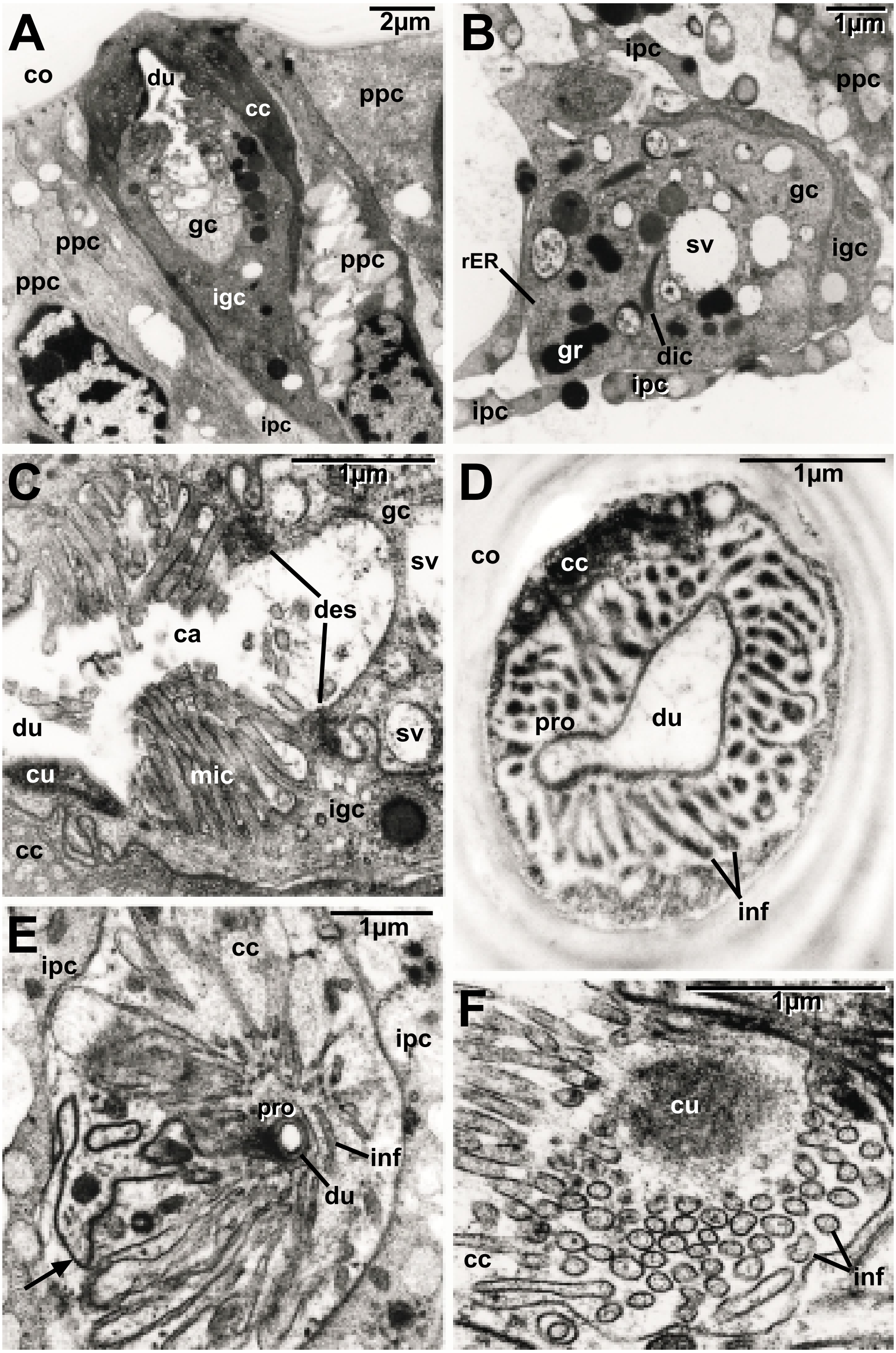
A small intermediary cell provides both the connection between the secretory gland and the distal canal cell and surrounds nearly the whole secretory gland cell body (Fig. 1A). The apex of the intermediary cell houses several microvilli bordering a widened extracellular cavity of the conducting canal, which is in connection with the most distal part of the secretory gland cell (Fig. 3C). Only in the most distal region of the extracellular cavity are the microvilli replaced by a cuticular intima, which is in contact with the cuticle of the pore canal. The dense cytoplasm of the intermediary cell, whose small nucleus is situated in the broadest part of the cell, is rich in rough ER and osmiophilic granules (Fig. 3A).

Canal cell

The canal cell occupies a distal position just below the corneal cuticle and surrounds the distal and median parts of both cell types described above (Fig. 1A). The canal cell forms a cuticular duct that traverses the cornea, then widens (Fig. 3D) and finally opens between the ommatidia. The cuticle is continuous with the epicuticle of the cornea. The material of the cuticle appears homogeneous and electron-lucent and is surrounded by an osmiophilic layer. The apical plasma membrane is intensely folded and forms deep microvilli-like projections, which surround the cuticular duct, but become smaller distally (Figs 3E, F). These apical infoldings are strengthened by microtubules. Homogeneous cuticular material is distributed between the microvillar infoldings (Fig. 3F). The cytoplasm of the canal cell contains a small nucleus of approximately 5 μm in diameter, numerous large osmiophilic secretory granules, and a weakly developed rough ER.

L. forficatus **(Lithobiomorpha)**

In *L. forficatus* somewhat similar interommatidial exocrine glands can be found. However, they differ from the type described above by forming clusters of two or three glandular units. Secondly, there is no evidence for the existence of an intermediary cell


A
2µm
co
du
cc
ppc
gc
ppc
ppc
ppc
igc
ipc
B
1µm
ipc
ppc
gc
sv
igc
rER
gr
dic
ipc
ipc
C
1µm
gc
sv
des
ca
du
sv
cu
mic
igc
cc
D
1µm
co
cc
pro
du
inf
E
1µm
ipc
cc
ipc
pro
inf
du
F
1µm
cu
cc
inf

and, therefore, every glandular unit includes only two different cell types, a proximal secretory gland cell and a distal canal cell (Fig. 1B).

Secretory gland cell

Secretory gland cells, varying in number from one to three, can be observed in the proximal regions of several interommatidial triangles always made up by three surrounding ommatidia. However, a consistent arrangement was not apparent. The number of secretory gland cells apparently depends on their position within the *Lithobius*-eye, whereas the clustered ones seem to be limited to the central region.

Each secretory gland cell is similarly drop-shaped as in *S. coleoptrata*. Its voluminous part is located most proximally, reaching the level of the nuclei of the proximal retinula cells. The small kidney-shaped nucleus is also located at this level. The rather electron-dense cytoplasm is enriched by dictyosomes, small osmiophilic vesicles, and an often circularly arranged rough ER (Fig. 4A). The lobe of the cell decreases continuously in volume, leading to distal regions, and usually contains a peripherally displaced rough ER, dictyosomes, and large, electron-dense and seemingly coalesced vesicles. The deeply infolded cell apex surrounds the basal lobe of the canal cell, which houses a small, cuticular duct (Fig. 4B).

A wide extracellular cavity could, however, not be determined. Distally the secretory gland cell is increasingly ensheathed by numerous thin processes of the interommatidial pigment cells (covering cells).

Canal cell

Up to three clustered canal cells are noticeable in a triangular space surrounded by three ommatidia (see fig. 4C). No regular pattern was apparent here either, but eye glands located in more marginal areas show mostly only a single canal cell.

The formation of a common cuticular duct, the occurrence of thin apical infoldings surrounding the cuticular duct, the cytoplasmic consistency, its content of organelles, its shape, as well as the proximal position of the nucleus, closely resemble the situation

Fig. 3. Transmission electron micrographs (TEM) showing fine structural details of the interommatidial exocrine gland within the facetted eye of *Scutigera coleoptrata*. **A.** Oblique-longitudinal section through distal region of an interommatidial space and the distal half of an interommatidial gland complex (bordered by interommatidial pigment and primary pigment cells). **B.** Transverse section through most proximal region of one secretory gland cell containing typical glandular organelles. A small remainder of the intermediary gland cell partly envelopes the voluminous lobe. **C.** Longitudinal section through extracellular cavity, representing proximal component of secretion-transporting system. **D.** Transverse section through most distal part of the canal cell containing the axial, widened cuticular gland ductule. Endocuticular lamellae of the cornea enclose the canal cell. Cuticular projections are homogenous and the main canal cells' cytoplasm is radially displaced, but a small proportion of the plasma is aggregated into thin foldings of apical plasma membrane. **E.** Transverse section through middle region of canal cell. The narrow cuticular ductule is located axially and homogenous material of the cuticle is distributed between cytoplasmatic infoldings. Note the organisation of the inner cell membrane (*arrow*), indicating the sheathing character of this cell type. **F.** Oblique-longitudinal section through middle part of canal cell. Cytoplasmatic infoldings are strengthened with microtubules. The cuticle of the axial gland ductule is cut only tangentially. *ca* = extracellular cavity, *cc* = canal cell, *co* = cornea, *cu* = cuticle, *des* = desmosomes (*Zonulae adhaerentes*), *dic* = dictyosome, *du* = cuticular gland ductule, *gc* = secretory gland cell, *gr* = osmiophilic secretory granules, *igc* = intermediary gland cell, *inf* = cytoplasmatic infoldings, *ipc* = interommatidial pigment cell, *mic* = microvilli, *ppc* = primary pigment cell, *pro* = cuticular projections, *rER* = rough endoplasmatic reticulum, *sv* = secretory vesicle.

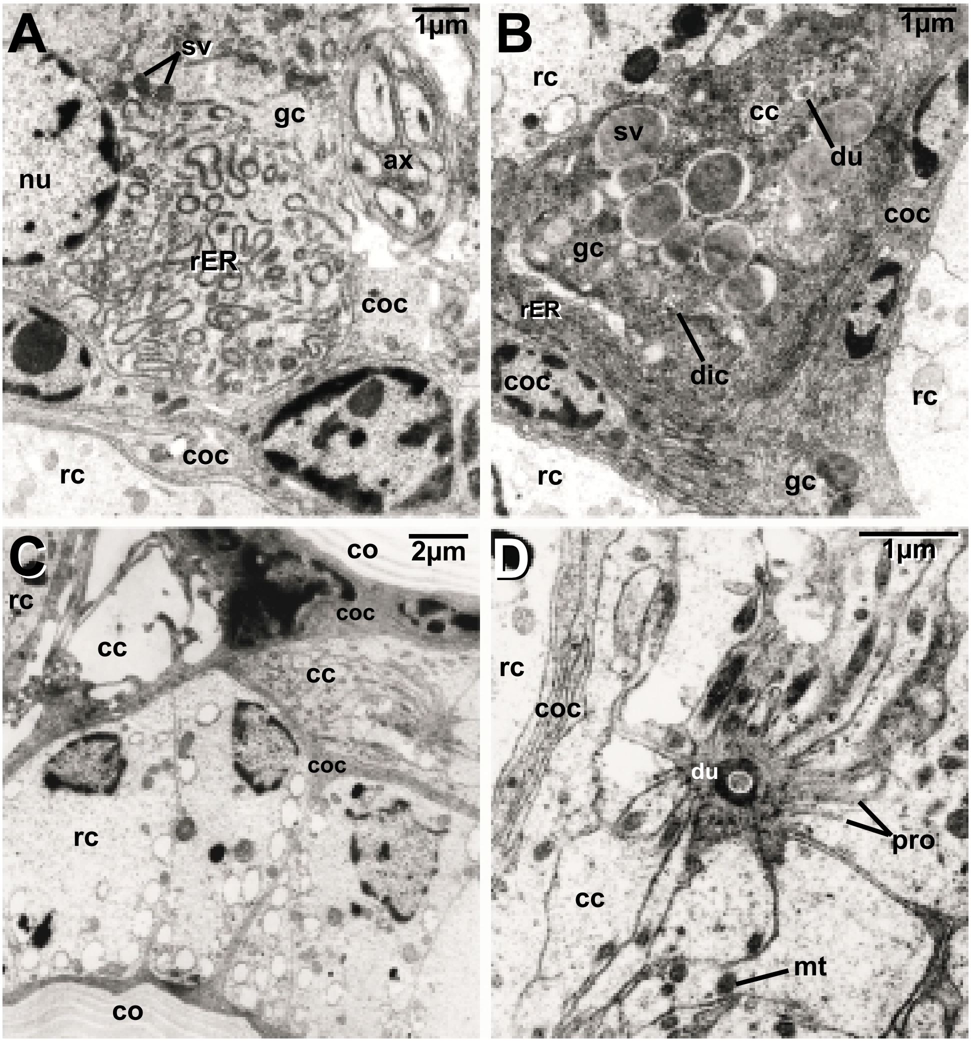


Fig. 4. Transmission electron micrographs (TEM), showing fine structural organisation of the interommatidial exocrine gland within the lateral compound eye of *Lithobius forficatus*. **A.** Transverse section through proximal region of one secretory gland cell containing typical glandular organelles. The gland cell lobe is surrounded by dense layers of covering and proximal (basal) retinula cells. **B.** Transverse section through distal region of two neighbouring, unequally sized secretory gland cells; the upper one being penetrated by a small proximal process of the canal cell with the cuticular gland ductule. **C.** Oblique-transverse section through a triangular interstitium in distal eye region. Two neighbouring, but not yet fused canal cells fill the interommatidial space and are surrounded by covering cells and distal retinula cells. **D.** Transverse section through middle part of one canal cell containing axially placed cuticular gland ductule. *ax* = nerve bundle, *cc* = canal cell, *co* = cornea, *coc* = covering (interommatidial pigment) cells, *dic* = dictyosome, *du* = cuticular gland ductule, *gc* = secretory gland cell, *mt* = mitochondrium, *nu* = nucleus, *pro* = cuticular projections, *rc* = retinula cell, *rER* = rough endoplasmatic reticulum, *sv* = secretory vesicle.

described above for the canal cells of *S. coleoptrata* (Fig. 4D). The proximal part of the canal cell envelopes, as well as penetrates, the apex of at least one secretory gland cell (Fig. 4B). The oblong nucleus lies beneath the transition zone of the distal and proximal retinula cells.

DISCUSSION

Epidermal exocrine glands between the ommatidia have never been described before in *S. coleoptrata*. Based on their fine structure it is obvious that these glands and the type of interommatidial exocrine gland found in *L. forficatus* correspond to class 3 epidermal glands as defined by Noirot & Quennedy (1974) and Quennedy (1998) for insect epidermal glands. Those epidermal glands are composed of several cells connected to the cornea by a cuticular duct which drains the secretion outside. As far as is known to date from electron microscopic investigations on Chilopoda, epidermal glands are structurally very diverse. The glands are composed of varying cell types of different numbers:

- Epidermal glands composed of two types of cells (secretory + canal): telopodal glands of Lithobiomorpha (Keil 1975), and ventral glands of Geophilomorpha (Turcato & Minelli 1990; Hopkin & Anger 1992). In *L. forficatus* additional exocrine glands are associated with the telopodal glands (Keil 1975). Exocrine glands are distributed in the vicinity of coxal organs (Rosenberg & Greven 1996); they surround the organ of Tömösvary (Tichy 1973), are associated with the antennal complex of sensilla trichoidea (Keil 1975 1976), and are distributed between the ommatidia of *L. forficatus* (this paper).
- Epidermal glands composed of three types of cells (secretory + intermediary + canal): interommatidial exocrine glands of *S. coleoptrata* (this paper); exocrine glands associated with the coxal organs in Lithobiomorpha, Scolopendromorpha and Geophilomorpha (Rosenberg 1985).
- Epidermal glands composed of four types of cells (secretory + intermediary + proximal canal + distal canal): maxillary organ gland of *S. coleoptrata* (Hilken *et al*. 2003).

The cuticle of the conducting canal is always formed by the canal cell(s). Canal cells are considered to be mostly secretory when microvillar differentiations of the apical plasma membrane are present, which surround the conducting canal. In intermediary cells a cuticle is only present in the most distal part of the conducting canal. In insect epidermal glands a cuticle is located in the extracellular space of the secretory cell and the conducting canal surrounded by one or more canal cells (Quennedy 1998). In Chilopoda, in contrast, no cuticular intima can be observed within the basal part of extracellular cavity formed by the apex of the secretory gland cell. A cuticle is only present in the most distal part of the conducting canal of the intermediary cell and in the conducting canal formed by the canal cells.

Similar interommatidial exocrine glands have been described in *L. forficatus* by Grenacher (1880) and termed integument glands. The fine structure and position of their canal and secretory cells appear to be almost identical to the eye glands of *S. coleoptrata*. On the basis of an average number of two secretory and canal cells, as well as the lack of intermediary gland cells, we suggest that a fused, secondarily derived exocrine eye gland type may be realised in *Lithobius*. Each single secretory gland cell, thereby, becomes fused with a single canal cell representing one module within an apparatus of a total of four cells. Proximally these modules are clustered, but not fused, and it is still an open question where the fusion exactly occurs. Since the number of up to three ascending cuticular ductules does not coincide with one pore opening per triangular interstitium, it seems likely that fusion occurs within the cornea or just beneath.

Despite these differences, we suggest that the interommatidial exocrine glands of the Lithobiomorpha are homologous to those of the Scutigeromorpha.

Phylogenetic implications

Recently, the monophyly of the main chilopod taxa Scutigeromorpha, Lithobiomorpha, Craterostigmophora, Scolopendromorpha and Geophilomorpha was confirmed by combined molecular/morphological data analyses by Edgecombe *et al*. (1999) and Edgecombe & Giribet (2002). The Pleurostigmophora concept formulated first by Verhoeff (1902) and afterwards confirmed by Dohle (1985) has recently been supported by molecular data (Giribet *et al*. 1999), combined molecular/morphological studies (Edgecombe *et al*. 1999; Edgecombe & Giribet 2002), as well as by some characteristics of the circulatory system (Wirkner & Pass 2002). In the light of the Pleurostigmophora concept, with the notostigmophoran Scutigeromorpha as a sister group to the Pleurostigmophora, and the Lithobiomorpha as most basal taxon within the latter, the presence of interommatidial exocrine glands within the Scutigeromorpha and Lithobiomorpha implies that such eye glands belonged to the ground pattern of the Chilopoda and had been lost in the lineage leading to Craterostigmophora, Scolopendromorpha and Geophilomorpha. The proposed presence of interommatidial exocrine glands in the ground pattern of Chilopoda might also imply that compound eyes or at least extended fields of ocelli were present. But following principles of homology, we assume that ancestral chilopods may have possessed compound eyes (Müller *et al*. in review) and, therefore, we prefer to speak about ommatidia for both taxa, Scutigeromorpha and Lithobiomorpha, instead of using the earlier term ‘lateral ocelli’. The loss of interommatidial exocrine glands could be considered a result of a phylogenetic series of eye transmissions leading from large compound eyes in Scutigeromorpha, to the formation of smaller compound eyes—‘lateral ocellar fields’—in Pleurostigmophora. The regression of the number of ommatidia within Pleurostigmophora appears to have started in Lithobiomorpha (e.g. 35–110 ommatidia in *L. forficatus*: Bähr (1971)), continued in Craterostigmophora and Scolopendromorpha (only few lateral ‘ocelli’), and ended in Geophilomorpha, resulting in a total reduction of ‘ocellar’ lens eyes. This evolutionary pathway agrees with Paulus (1986 2000), who illustrated several ommatidia-transforming mechanisms, which have occurred several times independently within the various groups of holometabolous insects and apparently have led to a high diversity of larval stemmata. Then, the loss of interommatidial exocrine glands within the stem lineage of Chilopoda could be related to the progressive shortage of interommatidial spaces. Secondly, the presence of those glands might, from a functional point of view, be only reasonable, if significant numbers of ommatidial ocelli were developed within the pleurostigmophoran eyes.

Functional considerations

In insects three principal functions are attributed to epidermal glands. They are suitable for: a) chemical defence, and useful in b) intraspecific communication by chemical signals (pheromones), and c) possibly involved in the deposition of the cement layer on the cuticle (Noirot & Quennedy 1974). In Chilopoda the function of most of the epidermal exocrine glands remains unclear. The telopodal glands and the sternal glands function as defensive glands, which secrete defensive substances as a response to attacks from predatory arthropods. In Geophilomorpha the defensive secretion is characterised as proteinaceous and either cyanogenic (Jones *et al.* 1976; Schildknecht *et al.* 1968) or without cyanide (Hopkin *et al.* 1990). The exocrine glands surrounding the coxal organs in Chilopoda secrete a carbohydrate-rich mucous layer. It has been suggested that this mucus consists of hygroscopic material, which would gather water vapour from the air (Rosenberg 1985; Rosenberg & Greven 1996). Blower (1951 1952) mentioned epidermal glands in Lithobiomorpha and Geophilomorpha, located especially in those regions of the body where the animals come into contact with solids of the environment. The glands appear to secrete lipoid materials which pass onto and across the surface of the cuticle to form a superficial layer, impregnating the exocuticle. Data based on some Lithobiomorphs are available, which point to the presence of a sex-specific coxal pheromone (Littlewood & Blower 1987). Such pheromones are thought to be produced exclusively by epidermal exocrine glands situated in the vicinity of the coxal organs (Rosenberg 1994).

Although the precise function of interommatidial exocrine glands in *S. coleoptrata* and in *L. forficatus* is still obscure, it seems likely that these glands produce anti-fungal or anti-bacterial substances that spread across the corneal surface and thus preserve clarity of the cornea. Bennet & Manton (1963) observed that epimorphic centipedes readily become infested with the resting stages of tyroglyphid mites. Such infestations have not occurred on *Lithobius* or *Scutigera*. It could be possible that the secretion of the interommatidial glands prevents attachment of ectoparasites on the ommatidial cornea. But as long as the composition of the secretion product of the interommatidial glands is not known, a functional explanation for the presence or absence of these glands, hitherto only found in Scutigeromorpha, Lithobiomorpha, possibly in an amphipod (Meyer-Rochow *et al.* 1991), and in a single archeaognathe species (Eisenbeis & Wichard 1985), appears speculative. We hope that our results and conclusions will lead to a renewed interest in chilopod vision in general and interommatidial exocrine glands in particular.

ACKNOWLEDGEMENTS:

For their considerable support we are grateful to Prof. Dr Ludwig Jonas and his employees working at the Electron Microscopic Centre of the Medical Faculty of the University of Rostock. Furthermore, we want to thank Prof. Dr Ragnar Kinzelbach (University of Rostock) and Dr Stefan Richter (Humboldt University of Berlin) for correcting our manuscript and giving numerous fruitful contributions to the discussion. We thank Dr Greg Edgecombe (Centre for Evolutionary Research, Australian Museum, Sydney) for his investigation of the ommatidial ocelli of *Australobius scabrior* and *Craterostigmus tasmanius*.

REFERENCES

Attems, K. 1926. Chilopoda. *In*: Kükenthal, W. & Krumbach, K eds, *Handbuch der Zoologie*, **4** (Myriapoda). Berlin: Walter de Gruyter pp. 239–402.

Ax, P. 1999. *Das System der Metazoa II. Ein Lehrbuch der phylogenetischen Systematik*. Stuttgart: Gustav Fischer Verlag pp. 216–229.

Bähr, R. 1971. Die Ultrastruktur der Photorezeptoren von *Lithobius forficatus* L. (Chilopoda, Lithobiidae). *Zeitschrift für Zellforschung und Mikroskopische Anatomie* **116**: 79–93.

Bennett, D. S. & Manton, S. M. 1963. Arthropod segmental organs and malpighian tubules, with particular reference to their function in the Chilopoda. *Annals and Magazine of Natural History (Ser. 13)* **5**: 545–556

Blower, J. G. 1951. A comparative study of the chilopod and diplopod cuticle. *Quarterly Journal of Microscopical Science* **92**: 141–161.

——— 1952. Epidermal glands in centipedes. *Nature (London)* **170**: 166–167.

Borucki, H. 1996. Evolution und Phylogenetisches System der Chilopoda (Mandibulata, Tracheata). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF)* **35**: 95–226.

Brade-Birks, H. K. & Brade-Birks, S. G. 1920. Notes on Chilopoda XX. Luminous Chilopoda, with special reference to *Geophilus carpophagus*, Leach. *The Annals and Magazine of Natural History (9. Ser.)* **5**: 1–30.

Dohle, W. 1985. Phylogenetic pathway in Chilopoda. *Bijdragen tot de Dierkunde* **55** (1): 55–66.

——— 1998. Myriapod-insect relationships as opposed to an insect-crustacean sister group relationship. *In*: Fortey, R. A. & Thomas, R. H., eds, *Arthropod relationships.* Systematics Association Special Volume Series 55. London: Chapman & Hall pp. 305–315.

Edgecombe, G. D. & Giribet, G. 2002. Myriapod phylogeny and the relationships of Chilopoda. *In*: Llorente Bousquets, J. & Morrone, J. J., eds, *Biodiversidad, Taxonomia y Biogeografia de Artrópodos de México: Hacia una síntesis de su Conocimiento*, Vol. III. México: Prensas de Ciencias, Universidad Nacional Autónoma de México pp. 143–168.

Edgecombe, G. D, Giribet, G. & Wheeler, W. C. 1999. Phylogeny of Chilopoda: combining 18S and 28S rRNA sequences and morphology. *In*: Melic, A., De Haro, J. J., Mendez, M. & Ribeira, I. eds, *Evolucíon y Filogenia de Arthropoda. Boletin de la Sociedad Entomológica Aragonesa* **26**: 293–331.

Eisenbeis, G. & Wichard, W. 1985. *Atlas zur Biologie der Bodenarthropoden*. Stuttgart: Gustav Fischer Verlag pp. 1–434.

Fahlander, K. 1938. Beiträge zur Anatomie und systematischen Einteilung der Chilopoda. *Zoologisca Bidrag Från Uppsala* **17**: 1–148.

Fuhrmann, H. 1922. Beiträge zur Kenntnis der Hautsinnesorgane der Tracheaten. I. Die antennalen Sinnesorgane der Myriapoden. *Zeitschrift für Wissenschaftliche Zoologie* **119**: 1– 52.

Giribet, G., Carranza, S., Riutort, M., Baguna, J. & Ribera, C. 1999. Internal phylogeny of the Chilopoda (Myriapoda, Arthropoda) using complete 18S rDNA and partial 28S rDNA sequences. *Philosophical Transactions of the Royal Society of London (Biological Sciences)* **354**: 215–222.

Grenacher, H. 1880. Über die Augen einiger Myriapoden. Zugleich eine Entgegnung an V. Graber. *Archiv für Mikroskopische Anatomie* **18**: 415–467.

Hilken, G., Brockmann, C. & Rosenberg, J. (2003). The maxillary organ gland: Description of a new head gland in *Scutigera coleoptrata* (Chilopoda, Notostigmophora). *African Invertebrates* **44** (1): 175–184.

Hopkin, S. P. & Anger, H. S. 1992. On the structure and function of the glue-secreting glands of *Henia vesuviana* (Newport, 1845) (Chilopoda, Geophilomorpha). *In*: Meyer, E., Thaler, K. & Schedl, W. eds, *Advances in Myriapodology, Proceedings of the 8th International Congress of Myriapodology. Berichte des Naturwissenschaftlich-Medizinischen Vereins zu Innsbruck* **10** (Suppl.): 71–80.

Hopkin, S. P., Gaywood, J. F. V., Vincent & Mayes-Harris, E. L. V. 1990. Defensive secretion of proteinaceous glues by *Henia* (*Chaetechelyne*) *vesuviana* (Newport) (Chilopoda, Geophilomorpha). *In*: Minelli, A. ed., *Proceedings of the 7th International Congress of Myriapodology*. Leiden: Brill pp. 175–181.

Jones, T. H., Conner, W. E., Meinwald, J., Eisner, H. E. & Eisner, T. 1976. Benzoyl cyanide and mandelonitrile in the cyanogenetic secretion of a centipede. *Journal of Chemical Ecology* **2**: 421–429.

Karnovsky, M. J. 1965. A formaldehyde-glutaraldehyde fixative of high osmolality for use in electron microscopy. *Journal of Cell Biology* **27**: 137–138.

Keil, T. 1975. Die Antennensinnes- und Hautdrüsenorgane von *Lithobius forficatus* L. Eine licht- und elektronenmikroskopische Untersuchung. Dissertation FB 23, FU-Berlin, pp. 1–61.

——— 1976. Sinnesorgane auf den Antennen von *Lithobius forficatus* L. (Myriapoda, Chilopoda).1. Die Funktionsmorphologie der Sensilla trichoidea. *Zoomorphologie* **84**: 77–102.

KOCH, A. 1927. Studien an leuchtenden Tieren: I. Das Leuchten der Myriapoden. *Zeitschrift für Morphologie und Ökologie der Tiere* **8**: 241–270.

LITTLEWOOD, P. M. H. & BLOWER, J. G. 1987. The chemosensory behaviour of *Lithobius forficatus*. 1. Evidence for a pheromone released by the coxal organs (Myriapoda: Chilopoda). *Journal of Zoology* **211**: 65–82.

MÜLLER, C. H. G., ROSENBERG, J., RICHTER, S. & MEYER-ROCHOW, B. 2003. The compound eye of *Scutigera coleoptrata* (Linnaeus, 1758) (Chilopoda: Notostigmophora): an ultrastructural re-investigation, which adds support to the "Mandibulata concept". *Zoomorphololgy* (in press).

MEYER-ROCHOW, V.B., STEPHAN, H. & MORO, S. D. 1991. Morphological and anatomical observations on the hairy eyes of males and females of the marine amphipod *Dulichia porrecta* (Crustacea; Amphipoda). *Bolletino di Zoologia* **58**: 59–69.

NOIROT, C. & QUENNEDY, A. 1974. Fine structure of insect epidermal glands. *Annual Review of Entomology* **19**: 61–80.

PAULUS, H. F.1986. Evolutionswege zum Larvalauge der Insekten – ein Modell für die Entstehung und die Ableitung der ozellären Lateralaugen der Myriapoda von Fazettenaugen. *Zoologische Jahrbücher* (*Abteilung Systematik*) **113**: 353–371.

——— 2000. Phylogeny of the Myriapoda – Crustacea – Insecta: a new attempt using photoreceptor structure. *Journal of Zoological Systematics and Evolutionary Research* **38**: 189–208.

QUENNEDY, A. 1998. Insect epidermal gland cells: Ultrastructure and morphogenesis. *In*: Harrison, F. W. &. Rice, M. E., eds, *Microscopic anatomy of invertebrates*, **11**A: Insecta. New York: Wiley-Liss pp. 177–207.

ROSENBERG, J. 1985. Untersuchungen zur feinstrukturellen Organisation und Funktion der Coxal- und Analorgane bei Chilopoden. *Bijdragen tot de Dierkunde* **55**: 337–344.

——— 1994. Fine structure of epidermal glands in vicinity to the coxal organs of *Lithobius forficatus* (Chilopoda). *Acta Biologica Benrodis* **6**: 37–47.

ROSENBERG, J. & GREVEN, H. 1996. Coxal organs of Chilopoda: The exocrine glands in *Lithobius forficatus*. *In*: Geoffroy, J. J., Mauries, J.-P. & Nguyen Duy-Jacquemin, M., eds, *Acta Myriapodologica*; *Memoires du Museum National d'Histoire Naturelle* (Paris) **169**: 403–409.

SCHILDKNECHT, H., MASCHWITZ, U. & KRAUSS, D. 1968. Blausäure im Wehrsekret des Erdläufers *Pachymerium ferrugineum*. XXXV. Mitteilung über Arthropoden-Abwehrstoffe. *Naturwissenschaften* **55**: 230.

TICHY, H. 1973. Untersuchungen über die Feinstruktur des Tömösvaryschen Sinnesorgans von *Lithobius forficatus* L. (Chilopoda) und zur Frage seiner Funktion. *Zoologische Jahrbücher* (*Abteilung Anatomie und Ontogenie der Tiere*) **91**: 93–139.

TURCATO, A. & MINELLI, A. 1990. Fine structure of the ventral glands of *Pleurogeophilus mediterraneus* (Meinert) (Chilopoda, Geophilomorpha). *In*: Minelli, A., ed., *Proceedings of the 7th International Congress of Myriapodology*. Leiden: Brill pp. 165–173.

VERHOEFF, K. W. 1902–1925. Chilopoda. *In*: Bronn, H. G. ed., *Klassen und Ordnungen des Tierreichs*, Vol.5. Leipzig: Akademische Verlagsgesellschaft pp. 1–725.

WIRKNER, C. S. & PASS, G. 2002. The circulatory system in Chilopoda: functional morphology and phylogenetic aspects. *Acta Zoologica* (*Stockholm*) **83** (3): 193–202.